

Foraging strategies and diet composition of two orb web spiders in rice ecosystems

Hafiz Muhammad Tahir: Department of Zoology, University of the Punjab, Lahore, Pakistan.
E-mail: hafiztahirpkl@yahoo.com

Abida Butt: Department of Zoology, University of the Punjab, Lahore, Pakistan

Sher Muhammad Sherawat: Department of Agriculture, District Sheikupura, Pakistan

Abstract. We conducted a field study in September 2007 and 2008 to analyze the foraging activity, natural diets, and predatory efficacy of *Tetragnatha javana* (Thorell 1890) (Araneae: Tetragnathidae) and *Neoscona theis* (Walckenaer 1842) (Araneae: Araneidae) on selected prey. The relationship between body measurements (carapace width, leg length, total body length, and body weight) and web dimensions (capture area, capture thread length, number of radii, number of spirals, and mesh height) of both species was also investigated. Most of the observed *T. javana* constructed their webs between two adjacent rice plants, while *N. theis* placed theirs at the top of rice plants. Both species required approximately an hour to complete a web, which differed significantly from each other in height, diameter, and capture area. Both species constructed only a single web per day. Web building activity of both species was intense from 17:00 to 18:00, while prey-handling activity was high from 19:00 to 20:00. In both species, peaks of feeding were recorded just after the peaks of prey handling (21:00). The main prey orders caught in the webs of both species were Lepidoptera, Diptera, Homoptera, Coleoptera, Hymenoptera, and Orthoptera. The time required to reach and capture lepidopteran (adults of stem borer and leaf folder) and homopteran prey was similar for both species. However, the time required to reach and capture orthopteran (grasshopper nymphs) prey was significantly longer for *T. javana* than for *N. theis*. Capture area increased with carapace width, and capture thread length increased with carapace width and body weight, while leg length and body length did not relate to either of these web variables. The number of radii, number of spirals, and mesh height did not correlate with any of the body size measurements. We concluded that both species can be used effectively to reduce insect pests of rice fields.

Keywords: Araneidae, agroecosystem, pest suppression, biological control

Spiders are among the most abundant predatory groups in rice ecosystems (Sebastian et al. 2005; Takashi et al. 2006; Tahir & Butt 2008). Most of them are polyphagous predators, able to feed on various insect pests of agricultural crops (Lang et al. 1999; Hanna et al. 2003; Schmidt et al. 2004; Takashi et al. 2006). Several studies clearly describe their role in reducing insect pests in rice fields (Xu et al. 1987; Ye & Wang 1987; Tanaka 1989; Jalaluddin et al. 2000). Spiders use a variety of methods to capture prey. Hunting spiders may actively pursue or ambush prey, while web building spiders present a unique case of “sit-and-wait” predation (Heiling 1999; Park et al. 1999). Orb web spiders are characterized by the use of a web to capture prey (Turnbull 1960; Kajak 1965). Prey capture success of web building spiders is also influenced by spider size (Eberhard 1990), web size (Sherman 1994), and web placement (Chacon & Eberhard 1980; Rypstra 1985) as well as specific web parameters such as strength (Lubin 1986), adhesiveness (Opell 1994), extensibility (Vollrath 1992), and mesh size (Rypstra 1982; Eberhard 1986).

Orb web spiders may trap more insects than they can consume. Silk of some orb web weavers attracts herbivorous insects that would normally be drawn to flowers and new leaves (Craig et al. 1996). Up to 1000 insects may be present in a web at a given moment, and many are left in the web to be eaten later (Nyffeler et al. 1994a). Small pests, such as thrips, midges, and aphids, may be caught and die in the webs of large spiders, only to be ignored by the spiders (Nentwig 1987; Landis et al. 2000). Web weaving spiders must anchor their prey-capture devices to the appropriate substratum in order to increase the effectiveness of their webs; complex habitats

provide appropriate sites for different sizes and types of webs in prey capture (Rypstra et al. 1999).

Orb webs have developed as an efficient means of capturing flying insects. The optical properties of these webs tend to reduce their visibility, especially in low-light and varying background conditions (Craig 1986), making detection and avoidance difficult (Robinson & Mirick 1971). There are numerous reports concerning prey captured by web building spiders (Heiling 1999; Ibarra-Nunez et al. 2001; Ceballos et al. 2005).

We designed the present study to understand the role of two nocturnal orb web spiders, *Tetragnatha javana* (Thorell 1890) and *Neoscona theis* (Walckenaer 1842), in the suppression of insect pests in rice fields. These species were selected because of their abundance in the rice ecosystems of central Punjab, Pakistan (Tahir & Butt 2008). The objectives of the study were to record the differences, if any, in web building, prey handling, and feeding activities of both orb web weavers, to study the relationship of body size measures (carapace width, leg length, total body length, and body weight) with various web characteristics (capture area, capture thread length, number of radii, number of spirals, and mesh height), and to record the difference in time elapsed to reach and capture prey blown experimentally into their webs. This study will help to understand the impact of these orb web spiders in the suppression of insect pests of rice.

METHODS

Study site.—The study was conducted in September 2007 and 2008 in rice fields at the agricultural research farm,

Sheikupura (31°43'N, 73°59'E). The rice variety grown was super basmati. At the time of the experiment, the average height of the plants in the fields was 131 ± 11 cm). During the course of the study, the temperature fell to approximately $27 \pm 4^\circ$ C at night, and rose to about $41 \pm 6^\circ$ C during the day. The relative humidity was highly variable (65–85%).

Field observations.—We identified *T. javana* and *N. theis* by consulting Barrion & Litsinger (1995). We conducted field observations on three different days in the third and fourth week of September (2007 and 2008), respectively, starting each day at 16:00 h. During the study period, sunset occurred between 18:00 and 18:30 h and sunrise between 05:00 and 06:00 h. To check the activities of spiders and their webs, we walked through the field every hour during 24 h to cover a 50×50 m plot (the walk required 20 to 25 min). At night, we used a flashlight covered with dark red plastic, because it neither attracted insect prey nor disturbed the spiders' natural photoperiod (Herberstein & Elgar 1994; Heiling 1999; Ceballos et al. 2005). On each walk we recorded adult female spiders present on rice plants with or without a web. Each spider's position was marked individually with a numbered piece of white plastic tied to the nearest twig. Spider activities recorded were resting, building a web, handling or eating a prey. Prey counted included both those fed upon at the hub and ones tangled in the web but not being fed upon. Prey items in the webs of spiders were identified to order.

Information regarding web diameter, web position (height from the ground and location on the rice plant), capture area, capture thread length, mesh size, number of radii, number of spirals, and time required to complete a web were also collected ($n = 50$ each year). To record the data, we removed spiders from the webs and sprayed their webs with a fine mist of water and cornstarch, using a knapsack hand sprayer (THS-119428) to improve the resolution. Similarly, carapace width, length of leg IV (coxa to tarsus), total length, and weight were also recorded. Since the data did not differ during the two years (for either species), they were pooled for statistical analysis.

To estimate the number of prey items per m^2 of rice plants, we quickly covered plants with two plastic bags, and then cut all plants just above the roots. Arthropod prey were sampled every two hours (three replicates). Each entire cut rice stem was brought to the laboratory and carefully examined for insects. Total webs per m^2 were also counted every two hours (three replicates).

The normality distribution of the data was analyzed with Kolmogorov-Smirnov tests before conducting further statistical analysis. Student *t*-tests were applied to normally distributed data. Relationships between body size (carapace width, leg length, body length, and weight) and web size (capture area, capture thread length, mesh size, number of radii and number of spirals) were analyzed using Pearson correlations (Minitab 13.3). Data are presented as mean \pm 1 SD.

Prey capture efficiency.—We conducted an experiment to record prey capture events in the field during the third week of September 2007. In order to record the prey-capture efficiency of web weaving spiders, we used four experimental prey types that are major rice insect pests in the study area: adults of whitebacked planthoppers *Sogatella furcifera* (Horvath), leaf

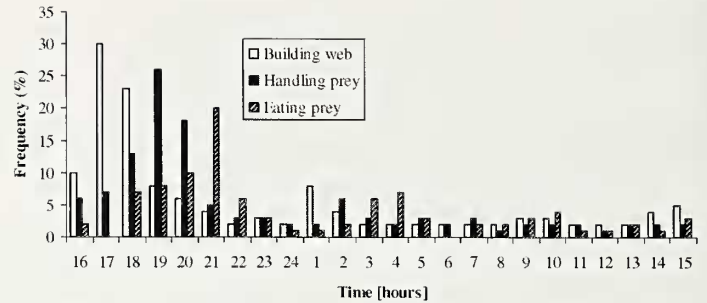


Figure 1.—Relative frequency of web building, prey handling, and feeding individuals of *Tetragnatha javana* each hour during 24 h in rice fields.

rollers *Cnaphalocrocis medinalis* (Guenee), white stem borers *Scirpophaga innotata* (Walker), and nymphs of grasshoppers *Hieroglyphus banian* (Fabricius). Twenty-five individuals of each prey type (plant hoppers: 3.4 ± 0.6 mm, grasshoppers: 10 ± 2.3 mm, stem borers $9 \text{ mm} \pm 2.4$ mm, leaf folders 10 ± 3.4 mm) were collected with a sweep net (42×80 cm, with a 90 cm handle) and a suction device (SIEMENS VK 20C01). Webs of adult females with no signs of prey were used in the experiment (Sebastian et al. 2005). Each prey animal was gently blown into the web with an inverted aspirator from 10 cm away. An average of twenty replicates was used for each type of prey, using a different web for each item. All prey were alive and undamaged before and after their introduction into the web. Once the prey contacted the web, we measured how long the spider needed to approach and capture the prey. Prey handling time began when the spider bit the prey, continued as the prey was manipulated, and ended when the spider took the prey to the hub. The predatory efficiency of both web-weaving spiders on four experimental prey types was compared using two-way ANOVA (SPSS 13). Subsequently, we conducted a Tukey HSD test separately for the time it took the spider to reach the prey and to capture it, with one factor being the spider species (2 levels) and the other being the prey species (4 levels).

RESULTS

***Tetragnatha javana*.**—A total of 214 spiders (123 in 2007 and 91 in 2008) and 135 webs (77 in 2007 and 58 in 2008) was observed during experimental periods of three days and nights. Although *T. javana* built webs at all hours of the day and night, their web building activity was most intense between 16:00 and 20:00 h (Fig. 1). Of the total observed, 59% completed web building between 17:00 and 18:00 h. *T. javana* constructed their webs between two adjacent rice plants and required 1 ± 0.3 h to complete a web. Webs averaged 109 ± 7.3 cm high and 29 ± 3.9 cm wide, $n = 50$ both years). After constructing a web *T. javana* occupied the center of the web and quickly attacked prey that attempted to escape.

Prey handling of *T. javana* was most intense between 19:00 and 20:00 h and decreased until 02:00 h, just after a second peak of web building. Feeding activity of *T. javana* was highest at 21:00 h, with a smaller peak between 03:00 and 04:00 h (Fig. 1). Combining both years, we observed 135 webs that contained 993 prey items (mean = 7.4 prey/web: Lepidoptera (41%), Diptera (24%), Homoptera (15%), Coleoptera (6%), Hymenoptera (3%), Orthoptera (3%), Araneae (3%) and unidentified prey (5%) (Table 1).

Table 1.—Relative frequency of pests recorded from the webs of *Tetragnatha javana* ($n = 993$) and *Neoscona theis* ($n = 849$).

Common name	Scientific name	<i>T. javana</i>	<i>N. theis</i>
Lepidoptera			
Yellow stem borer	<i>Scirpophaga incertulas</i> (Walker)	14	11
White stem borer	<i>Scirpophaga innotata</i> (Walker)	12	13
Pink stem borer	<i>Sesamia inferens</i> (Walker)	4	3
Stripped borer	<i>Chilo suppressalis</i> (Walker)	3	2
Sorghum stem borer	<i>Chilo partellus</i> (Swinhoe)	1	—
Leaf folder	<i>Cnaphalocrocis medinalis</i> (Guenee)	5	4
Leaf folder	<i>Mythimna separata</i> (Walker)	2	3
Homoptera			
Whitebacked planthopper	<i>Sogatella furcifera</i> (Horvath)	7	9
Green leafhopper	<i>Nephotettix nigripictus</i> (Stal.)	4	4
White leafhopper	<i>Cofana spectra</i> (Distant)	4	3
Diptera			
Rice gall midge	<i>Pachydiplosis oryzae</i> (W.-M.)	14	14
Rice shoot fly	<i>Atherigona oryzae</i> (Mall.)	6	4
Rice shoot fly	<i>Atherigona soccata</i> (Rond.)	3	3
Mosquito	<i>Culex</i> spp.	1	—

Density of potential prey increased after 16:00, reached a maximum at 20:00, and then declined until 04:00. Frequency of prey handling increased with density of potential prey ($r = 0.63$; $P < 0.01$, Fig. 1).

Neoscona theis.—We observed 141 spiders (73 in 2007 and 68 in 2008) and 97 webs (57 in 2007 and 40 in 2008). Of these, 63% completed web building between 17:00 and 18:00 h. Web building activities decreased but did not cease throughout the night (Fig. 2). Most *N. theis* (67%) constructed their webs at the top of rice plants and required 1 ± 0.4 h to build their webs. The hub of the web averaged 128 ± 7.0 cm above the ground, and the average diameter of the web was 34 ± 4.7 cm ($n = 50$ both years).

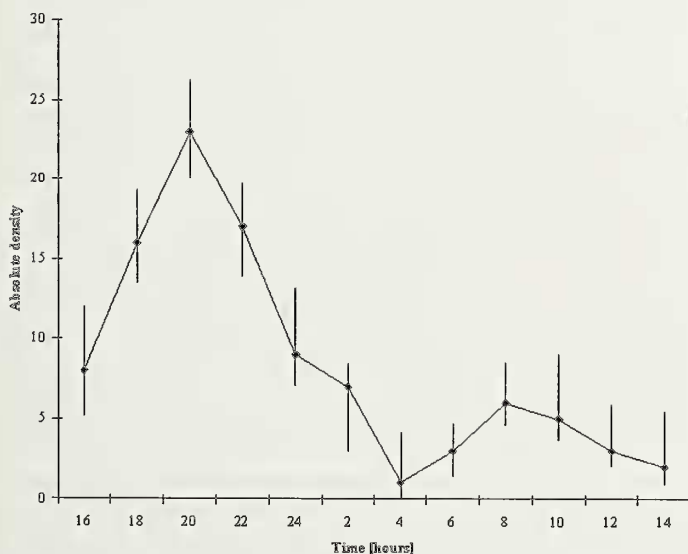


Figure 2.—Mean density (\pm SD) of potential prey per 1 m^2 of rice fields recorded at each two-hour period during 24 h (combined for both years).

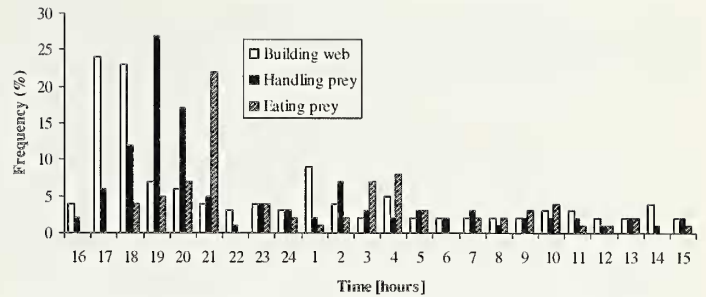


Figure 3.—Relative frequency of web building, prey handling, and feeding individuals of *Neoscona theis* each hour during 24 h in rice fields.

Prey handling activity of *N. theis* was most intense between 19:00 and 20:00 h, and increased slightly again around 02:00 h, just after the second highest frequency of web building. Feeding peaked at 21:00 h, 1 h after peak prey handling activity. A second minor peak in feeding occurred between 03:00 and 04:00 h. Web building, prey handling, and feeding activities of *N. theis* decreased before 06:30 (Fig. 3).

A total of 849 insects was recorded from 97 webs, an average number of 8.8 prey/web over the two years combined, consisting of Lepidoptera (36%), Diptera (21%), Homoptera (16%), Coleoptera (8%), Orthoptera (8%), Hymenoptera (4%), Araneae (4%), and unidentified prey (3%) (Table 1). Frequency of prey handling increased with density of potential prey ($r = 0.59$; $P < 0.01$, Fig. 3).

Predatory efficacy.—The time required for the two spiders to reach prey differed (two-way ANOVA: $F_{1, 23} = 29.54$, $P < 0.01$, Table 2). Time to reach prey also differed among four prey types ($F_{3, 23} = 359.93$, $P < 0.001$). Similarly, the time to capture prey differed between the two species ($F_{1, 23} = 209.33$, $P < 0.001$), as well as among the four prey types ($F_{3, 23} = 296.41$, $P < 0.001$, Table 3). Differences were due to the handling of orthopteran prey (Tukey HSD test).

Relationship of body size and web design.—The web design of adult females of both species correlated differently with the various body size measurements (Table 4). Capture areas of both species' webs increased significantly with carapace width ($r = 0.51$, $P < 0.01$ for *T. javana*; $r = 0.54$, $P < 0.01$ for *N. theis*), and capture thread length increased significantly with carapace width ($r = 0.55$, $P < 0.01$ for *T. javana*; $r = 0.62$, $P < 0.01$ for *N. theis*), and body weight ($r = 0.60$, $P < 0.01$ for *T. javana*; $r = 0.68$, $P < 0.01$ for *N. theis*). Leg length and body length did not correlate with these two web variables. Neither did the number of radii, number of spirals, and mesh height correlate with any of the four measurements of body size ($P > 0.05$). Comparison of web height, diameter, and capture area of the two species differed significantly ($t_{48} = 4.24$, $P < 0.01$; $t_{48} = 3.87$, $P < 0.01$; $t_{48} = 11.9$, $P < 0.001$, respectively). However, the number of spirals and number of radii in the webs of these two orb web spiders did not differ significantly ($t_{48} = 0.42$, $P > 0.05$; $t_{48} = 0.72$, $P > 0.05$, respectively).

DISCUSSION

This study suggests that most individuals of both species started to build their webs just after sunset, and kept the activities of web building, prey handling, and prey eating to a minimum after sunrise. Most individuals of both species fed

Table 2.—Mean time (s, \pm SE) to reach four prey types by *Tetragnatha javana* and *Neoscona theis*. Row-wise comparisons were done by Tukey HSD test. * $P < 0.005$; ns = non significant.

Prey type	<i>T. javana</i>	<i>N. theis</i>	Comparison
<i>Scripophaga imnotata</i> (Walker)	9.5 \pm 1.0	12.1 \pm 1.3	ns
<i>Cnaphalocrocis medinalis</i> (Guenee)	8.1 \pm 2.1	11.7 \pm 3.1	ns
<i>Sogatella furcifera</i> (Horvath)	9.1 \pm 2.2	11.4 \pm 2.0	ns
<i>Hieroglyphus banian</i> (Fabricius)	31 \pm 1.4	14.2 \pm 3.5	*

throughout the observation period; they seem to have a strategy to "build, catch, and eat" in a short period (Ceballos et al. 2005). Prey handling rates were highest at the beginning of the night in both species due to the high level of prey activity at this time (Kraker et al. 1999). Prey handling decreased after 20:00, which might be due to decreased activity of the prey after 20:00.

Both spiders took less time to reach and capture adult stem borers, leaf folders, and planthoppers than grasshopper nymphs in the prey capture efficacy experiment. This difference might be due to lower efficiency of their venom. Small prey were usually paralyzed more quickly than larger ones.

Although the main prey items of both web weavers were Lepidoptera, they both also fed on Diptera, Homoptera, Hymenoptera, Coleoptera, and Orthoptera. A comparable composition (insect orders) of potential prey for the web building spiders *Araneus diadematus* Clerck 1757 and *Argiope bruennichi* (Scopoli 1772) was described by Ludy (2007). These insect orders make up the majority of prey of spiders in rice agroecosystems. A varied diet creates an optimal, balanced nutrient composition needed for survival and reproduction (Greenstone 1979; Toft 1995). However, prey groups were not caught in the spider webs in proportions to their availability in the habitat. For example, we recorded 180 plant hoppers from 1 m² of experimental rice field during a high abundance period in the last week of September, but only 21 (11.7%) from the webs in this area.

Members of insect orders with good vision and maneuverability in flight, such as Diptera and Hymenoptera (Land 1997), may detect and evade webs, resulting in an underrepresentation there. However, good vision and maneuverability in flight is not important in the present study because both of the species captured prey mainly during night when visibility was low. Small and slow-flying insects with relatively large surface areas may be caught in spider webs most easily

Table 3.—Mean time (s, \pm SE) to capture four prey types by *Tetragnatha javana* and *Neoscona theis*. The prey capture started from the first contact with the prey and ended when the spider took the prey to the hub. Row-wise comparisons were done by Tukey HSD test. * $P < 0.005$; ns = non significant.

Prey type	<i>T. javana</i>	<i>N. theis</i>	Comparison
<i>Scripophaga imnotata</i> (Walker)	19.2 \pm 3.0	24.4 \pm 1.7	ns
<i>Cnaphalocrocis medinalis</i> (Guenee)	23.4 \pm 2.6	27.0 \pm 0.0	ns
<i>Sogatella furcifera</i> (Horvath)	19.7 \pm 2.1	17.0 \pm 4.3	ns
<i>Hieroglyphus banian</i> (Fabricius)	84.2 \pm 12.8	42.4 \pm 5.1	*

Table 4.—Summary of web characteristics and body measurements (mean \pm SE) of adult females of *Tetragnatha javana* and *Neoscona theis*.

Characteristic	<i>T. javana</i>	<i>N. theis</i>
Web height (cm)	109.7 \pm 7.3	128.0 \pm 7.0
Web diameter (cm)	29.3 \pm 3.9	34.0 \pm 5.0
Capture area (cm ²)	91.1 \pm 9.4	126.7 \pm 16.3
Number of radii	15.0 \pm 3.0	17.0 \pm 4.0
Number of spirals	22.0 \pm 4.0	27.0 \pm 4.0
Mesh height (mm)	1.6 \pm 0.6	2.7 \pm 0.3
Carapace width (mm)	1.0 \pm 0.3	1.9 \pm 0.4
Leg IV length (mm)	12.0 \pm 1.4	11.0 \pm 1.5
Total length (mm)	11.5 \pm 0.5	7.4 \pm 1.3
Wet weight (mg)	13.0 \pm 7.34	110.7 \pm 39.0

(Kajak 1965; Nentwig 1982, 1985). In the present study, more than 70% of the prey caught in the webs of both spiders belonged to the Lepidoptera, Diptera and Homoptera. More than 90% of the prey items recorded from the webs of both species were insects - the remaining 10% were spiders and unidentified prey. The difference in abundance of prey at different times is due to the difference in activity of insects at those times.

The webs of orb weaving spiders vary greatly in design; scientists have interpreted this variation as specialization for the capture of specific prey types (Walker 1992). Much of the interspecific variation in web architecture is related to factors other than prey types, including amount or shape of available space, presence of conspecifics, lack of previous experience at a website, presence or absence of water immediately below the orb, amount of silk available in the glands, and time of day (Eberhard 1990). Webs of smaller spiders, which are generally made with thinner threads and less adhesive, have reduced abilities to capture large prey (Eberhard 1990). Variation in web design (position, height, capture area, number of radii, hub position, number of spirals) of both species, as well as variation within species, was also recorded in this study. The general web architecture is thought to be genetically determined (Foelix 1992). Capture area and capture thread length increased significantly with carapace width in this study, a result also reported by Heiling et al. (1998). A large capture area results in high prey interception (Chacon & Eberhard 1980), and by increasing the distance between sticky spirals, spiders may enlarge the overall capture area without increasing their energy expenditure (Herberstein et al. 2000). Our result is in accordance with previous studies that also found a positive relationship between carapace width and web size (Eberhard 1988; Heiling et al. 1998). Mesh height did not relate to any of the body measurements in the present study, contrasting with the results of Eberhard (1988), who found leg length to be a good indicator of mesh height. Numerous field studies have also failed to find a consistent relationship between mesh height and prey size (Herberstein & Elgar 1994; Herberstein & Heiling 1998). A narrow mesh may facilitate the retention of larger prey, as more threads are in contact with the item (Eberhard 1990). However, more spiral turns also reflect more light, thus increasing the visibility of the web to the prey (Craig 1986; Craig & Freeman 1991). Mesh height may therefore indicate a compromise between prey retention and web visibility.

The possible role of these spiders in pest control can be estimated with simple calculations. The average number of pests and webs from 1 m² of rice fields of Punjab were 140 and 3.5, respectively. The average number of pests recorded from a single web of *T. javana* was 7.4, while the average number of pests collected from a single web of *N. theis* was 8.8. Thus, these two web builders (*T. javana* and *N. theis*) can produce up to a 22% reduction of the total pest population per day. Furthermore, many other spider species and other natural predators also contribute to the suppression of insect pests in the rice ecosystem. Both spiders studied can reduce the populations of insect pests in rice fields and may be useful in biological control of rice insect pests in Pakistan. However, in order to use them as biological control agents on a broader scale, further knowledge of their feeding habits, web construction behavior, reproductive strategies, prey preferences, and response to insecticides and herbicides is needed.

ACKNOWLEDGMENTS

The research was supported by the Department of Zoology, University of the Punjab, Lahore, Pakistan. Stano Pekár and two anonymous reviewers provided very useful and relevant comments on an earlier version of manuscript.

LITERATURE CITED

- Barrion, A.T. & J.A. Litsinger. 1995. Rice land spiders of South and Southeast Asia. CAB International, Wallingford, Oxfordshire, UK.
- Ceballos, L., Y. Henaut & L. Legal. 2005. Foraging strategies of *Eriophora edax* (Araneae, Araneidae): a nocturnal orb-weaving spider. *Journal of Arachnology* 33:509–515.
- Chacon, P. & W.G. Eberhard. 1980. Factors affecting numbers and kinds of prey caught in artificial spider webs, with consideration of how orb webs trap prey. *Bulletin of the British Arachnological Society* 5:29–38.
- Craig, C.L. 1986. Orb-web visibility: the influence of insect flight behaviour and visual physiology on the evolution of web designs within the Araneioidea. *Animal Behaviour* 34:54–68.
- Craig, C.L. & C.R. Freeman. 1991. Effect of predator visibility on the prey encounter: a case study on aerial web weaving spiders. *Behavioral Ecology and Sociobiology* 29:249–254.
- Craig, C.L., R.S. Weber & G.D. Bernard. 1996. Evolution of predator prey systems: spider foraging plasticity in response to the visual ecology of prey. *American Naturalist* 147:205–229.
- Eberhard, W.G. 1986. Effect of orb-web geometry on the prey interception and retention. Pp. 70–100. *In Spiders: Webs, Behavior and Evolution*. (W. Shear, ed.). Stanford University Press, Stanford, California.
- Eberhard, W.G. 1988. Behavioral flexibility in orb web construction: effect of supplies in different silk glands and spider size and weight. *Journal of Arachnology* 16:295–302.
- Eberhard, W.G. 1990. Function and phylogeny of the spider webs. *Annual Review of Ecology and Systematics* 21:341–372.
- Foelix, R.F. 1992. *Biologie der Spinnen*. Edition 2. Thieme, Stuttgart.
- Greenstone, M.H. 1979. Spider feeding behaviour optimizes dietary essential amino acid composition. *Nature* 282:501–503.
- Hanna, R., G.F. Zalom & J.W. Roltsch. 2003. Relative impact of spider predation and cover crop on population dynamics of *Erythroneura variabilis* in a raisin grape vineyard. *Entomologia Experimentalis et Applicata* 107:177–191.
- Heiling, A.M. 1999. Why do nocturnal orb-web spiders (Araneidae) search for light? *Behavioral Ecology and Sociobiology* 46:43–49.
- Heiling, A.M., M.E. Herberstein & G. Spitzer. 1998. Calculation of capture thread length in orb webs: evaluation of a new formula. *Annals of the Entomological Society of America* 91:135–138.
- Herberstein, M.E. & M.A. Elgar. 1994. Foraging strategies of *Eriophora transmarina* and *Nephila plumipes* (Araneae): nocturnal and diurnal orb-weaver spiders. *Australian Journal of Ecology* 19:451–457.
- Herberstein, M.E., A.C. Gaskett, D. Glencross, S. Hart, S. Jaensch & M.A. Elgar. 2000. Does the presence of potential prey affect web design in *Argiope keyserlingi* (Araneae, Araneidae)? *Journal of Arachnology* 28:346–350.
- Herberstein, M.E. & A.M. Heiling. 1998. Does mesh height influence prey length in orb-web spiders? *European Journal of Entomology* 95:367–371.
- Ibarra-Núñez, G., J.A. Garcia, J.A. Lopez & J.P. Lachaud. 2001. Prey analysis in the diet of some ponerine ants (Hymenoptera: Formicidae) and web-building spiders (Araneae) in coffee plantations in Chiapas, Mexico. *Sociobiology* 37:723–756.
- Jalaluddin, S.M., R. Mohan, R. Velusamy & S. Sadakathulla. 2000. Predatory behaviour in rice varieties under sodic soil conditions. *Entomology* 25:347–350.
- Kajak, A. 1965. An analysis of food relations between the spiders *Araneus cornutus* Clerck and *Araneus quadratus* Clerck and their prey in meadows. *Ekologia Polska Series A* 13:717–764.
- Kraker, J.D., V.A. Huis, L.K. Heong, J.C.V. Van Lenleren & R. Robbinge. 1999. Population dynamics of rice leafhopper and their natural enemies in irrigated rice fields in Philippines. *Bulletin of Entomological Research* 89:411–421.
- Land, M.F. 1997. Visual acuity in insects. *Annual Review of Entomology* 42:147–177.
- Landis, D.A., S.D. Wratten & G.M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* 45:175–201.
- Lang, A., J. Filser & J.R. Henschel. 1999. Predation by ground beetles and wolf spiders on herbivorous insects in maize crop. *Agriculture, Ecosystems & Environment* 72:189–199.
- Lubin, Y.D. 1986. Web building and prey capture in the Uloboridae. Pp. 132–171. *In Spiders: Webs, Behavior and Evolution*. (W. Shear, ed.). Stanford University Press, Stanford, California.
- Ludy, C. 2007. Prey selection of web building spiders (Araneidae) on field margins. *Agriculture, Ecosystems & Environment* 119:368–372.
- Nentwig, W. 1982. Why do only certain insects escape from a spider's web? *Oecologia* 53:412–417.
- Nentwig, W. 1985. Prey analysis of four species of tropical orb-weaving spiders (Araneae: Araneidae) and a comparison with araneids of the temperate zone. *Oecologia* 66:580–594.
- Nentwig, W. 1987. The prey of spiders. Pp. 249–263. *In Ecophysiology of Spiders*. (W. Nentwig, ed.). Springer-Verlag, Berlin.
- Nyffeler, M., W.L. Sterling & D.A. Dean. 1994. How spiders make a living. *Environmental Entomology* 23:1357–1367.
- Opell, B.D. 1994. Increased stickiness of prey threads accompanying web reduction in the spider family Uloboridae. *Functional Ecology* 8:85–90.
- Park, T.S., J. Jeon, H.K. Lim, S. Lee & J.C. Choe. 1999. Web orientation in a golden orb-web spider *Nephila clavata* (Araneae; Tetragnathidae). *Korean Journal of Biological Science* 3:161–165.
- Robinson, M.H. & H. Mirick. 1971. The predatory behavior of the golden-web spider *Nephila clavipes* (Araneae: Araneidae). *Psyche* 78:123–139.
- Rypstra, A.L. 1982. Building a better insect trap: an experimental investigation of prey capture in a variety of spider webs. *Oecologia* 52:31–36.
- Rypstra, A.L. 1985. Aggregations of *Nephila clavipes* (L.) (Araneae, Araneidae) in relation to prey availability. *Journal of Arachnology* 13:71–78.
- Rypstra, A.L., P.E. Carter, R.A. Balfour & S.D. Marshall. 1999. Architectural modifications of agricultural habitats and their impact on the spider inhabitants. *Journal of Arachnology* 27:371–377.

- Schmidt, M.H., C. Thies & T. Tschardtke. 2004. Landscape context of arthropod biological control. Pp. 55–63. *In* Ecological Engineering for Pest Management: Advances in Habitat Manipulation for Arthropods. (G.M. Gurr, S.D. Wratten & M.A. Altier, eds.). CSIRO Press, Collingwood, Australia.
- Sebastian, A.P., M.A. Thew, B.S. Pathummal, J. Joseph & R.C. Biju. 2005. The spider fauna of the irrigated rice ecosystem in central Kerala, India across different elevational ranges. *Journal of Arachnology* 33:247–255.
- Sherman, P.M. 1994. The orb-web: an energetic and behavioural estimator of spider's dynamic foraging and reproductive strategies. *Animal Behaviour* 48:19–34.
- Tahir, H.M. & A. Butt. 2008. Activities of spiders in rice fields of central Punjab, Pakistan. *Acta Zoologica Sinica* 54:701–711.
- Takashi, M., I. Chikara, T. Motonori, M.T. Mihoko, T. Ayame & K. Yasuhisa. 2006. Effects of tillage practices on spider assemblage in rice paddy fields. *Applied Entomology and Zoology* 41:371–381.
- Tanaka, K. 1989. Movements of spiders in arable land. *Plant Protection* 43:34–39.
- Toft, S. 1995. Value of the aphid *Rhopalosiphum padi* as food for cereal spiders. *Journal of Applied Ecology* 32:552–560.
- Turnbull, A.L. 1960. The prey of the spider *Linyphia triangularis* (Clerck) (Araneae: Linyphiidae). *Canadian Journal of Zoology* 38:859–873.
- Vollrath, F. 1992. Spider webs and silks. *Scientific American* 266(3): 46–52.
- Walker, J.R. 1992. What do orb webs catch? *Bulletin of the British Arachnological Society* 9:95–98.
- Xu, J.S., Z.F. Chen & R.L. Zhu. 1987. Study and application of spiders in rice fields in Zhejiang Province. *Natural Enemy* 9:140–144.
- Ye, Z.X. & D.D. Wang. 1987. Population dynamics of spiders in rice fields of Jiangxi Province. *Bulletin of Biological Control* 3:11–14.

Manuscript received 19 October 2008, revised 2 May 2009.